Chlorophyll-specific scattering coefficient of phytoplankton. A simplified theoretical approach

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**Abstract**—When studying the links between the optical properties of a water body and its phytoplankton content, it is convenient to use and necessary to study the "chlorophyll-specific" absorption and scattering coefficients for algae, respectively, $a^*$ and $b^*$. While $a^*$ is beginning to be well documented, little information is available on $b^*$ and its possible variations from one species to another. This paper deals with the chlorophyll-specific scattering coefficient, and presents a simple theoretical treatment developed with a view to explaining the possible changes of $b^*$ with the size of the algal cells and their intracellular chlorophyll concentration. In spite of its simplified character, this approach accounts for the unexpectedly large variations in $b^*$ as observed for algae grown in culture. These predictions and results are compared to the $b^*$ values derived for natural assemblages of phytoplankton in the marine environment.

**Introduction**

The process of light scattering by phytoplankters can be accounted for by its dependence upon the size (or the size distribution) of the cells and the refractive and absorptive properties of the cell material. The spectral behaviour of the efficiency factors for attenuation and scattering can be modeled with reasonably successful results (Bricaud and Morel, 1986), even if simplifying assumptions (sphericity and homogeneity of the cells) are made.

Without discussing the models or theories in detail, useful rules concerning the chlorophyll-specific scattering coefficient can be derived from very simple considerations. This coefficient, denoted $b^*$, is similar to the chlorophyll-specific absorption coefficient, $a^*$. It is defined as that part of the scattering coefficient of an algal suspension (or of a water body) which is due to the presence of algal cells, $b_c$, once it has been divided by the chlorophyll concentration, $C$:

$$b^* = b_c/C.$$ 

The specific absorption coefficient is of obvious interest for marine biologists or physiologists. In the sea or in culture, the amount of radiant energy which is captured by algae before utilized for photosynthesis, is expressed as $a^* C \dot{E}$, where $\dot{E}$ is the available radiant energy, in terms of scalar irradiance $\dot{E}$ (for symbols and definitions of the radiometric quantities, see Morel and Smith, 1982). For that reason $a^*$, often referred to

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as "\(k_c\)" has been the subject of many investigations [see Table 9.1 in Kirk (1983) and review in Bannister and Weidemann (1984)]. Conversely, the chlorophyll-specific scattering coefficient, not directly involved in the light harvesting process, has been scarcely studied and only recently have data appeared (Briculaud et al., 1983; Davies-Colley et al., 1986). However, both absorption and scattering processes are equally important in governing the transformations which the light field undergoes within the photic layer. In that sense, the scattering capabilities of algae, as they contribute to modify the light field, indirectly react on the actual absorption capabilities.

The vertical attenuation coefficient for downwelling irradiance (and hence the thickness of the euphotic layer) has been explicitly related to the absorption and scattering coefficients and relationships between these coefficients have been obtained by Monte-Carlo calculations (Gordon et al., 1975; Kirk, 1981). When trying to relate the irradiance attenuation within a layer to its algal content, it is therefore necessary to estimate the contribution of phytoplankton (depicted by the chlorophyll concentration) not only to the absorption, but also to the scattering coefficient of the medium. Kirk (1983, pp. 217–218) recently pointed out this need "... Scattering contributes in various ways to vertical attenuation of irradiance ... Little data is (sic) available on the scattering of algae. It seems reasonable, however, to suppose that the amount of scattering—especially per unit chlorophyll \(a\)—can vary markedly from one species to another."

The ocean colour (or more precisely the ocean spectral reflectance), as remotely sensed, is another example of an optical property which can be interpreted in terms of phytoplankton (Chl \(a\)) concentration. The reflectance of the upper ocean is linked to the backscattering and absorption coefficients of the water through their ratio, \(b/a\) (Gordon et al., 1975; Morel and Prieur, 1977). To analyse the effect of algal cells on reflectance it is again necessary to quantify their influence upon both the backscattering and absorption coefficients. Their partial contributions to these coefficients are, respectively, the quantities

\[
\tilde{b}_b b^* C
\]

and

\[
a^* C,
\]

where \(\tilde{b}_b\) is the ratio of the backscattering to the scattering coefficient. Values for this ratio in the case of algae have been proposed elsewhere (Morel and Briculaud, 1981b; Briculaud and Morel, 1986). The specific coefficients \(a^*\) and \(b^*\), on a per unit Chl \(a\) basis, must be known to explain or predict ocean reflectance as a function of the primary producers abundance.

Beside their optical effect on the medium, the light scattering properties of the algal cells are themselves of direct interest. Together with fluorescence properties, they provide information concerning the size and composition of individual cells (see e.g. Yentsch et al., 1983; Olson et al., 1985). The flow cytometric analysis of phytoplanktonic communities and the cell sorting are new powerful techniques which require a better knowledge of the optics of the algal cells, including their light scattering properties (Spinrad and Brown, 1986).

The aims of this paper are: (i) to present simple theoretical considerations concerning the possible variations of \(b^*\) according to the main characteristics of the algal cells; (ii) to examine whether such a simplified approach can account for global variations of \(b^*\) as
observed for different species grown in culture; (iii) to compare these results to those obtained for natural assemblages in the marine environment.

**THEORETICAL BACKGROUND**

This discussion is closely related to that set out for the specific absorption (Morel and Briceaud, 1981a), and a possible approach is suggested in Appendix 2 of this reference.

The scattering coefficient, \( b \) (dimension \( L^{-1} \)), which results from the presence of \( N \) equally sized particles in a volume \( V \) of the medium is

\[
b = (N/V)Q_{bs},
\]

where \( Q_{bs} \) is the dimensionless efficiency factor for scattering, i.e. the ratio of the radiant energy scattered from the particle to the energy impinging on its geometrical cross-section, \( s \). By assuming that these equally sized particles are spherical with a diameter \( d \), the cross-sectional area \( s \) is equal to \((\pi/4) \ d^2\). These particles (algal cells) contain a certain amount of Chl \( a \). The intracellular concentration of this pigment is denoted by \( c_i \). The concentration within the suspension, \( C \), is linked to \( c_i \) by

\[
C = (N/V) \ c_i \ v,
\]

where \( v = (\pi/6) \ d^3 \) is the volume of the individual particles. The specific scattering coefficient \( b^* \) (dimension \( L^2 \ M^{-1} \)) is therefore

\[
b^* = b/C = (s/vc_i) \ Q_{bs}
\]

or

\[
b^* = (3/2) \ (1/dc_i) \ Q_{bs}.
\]

For non-spherical particles, the \( s \) to \( v \) ratio would be different, \( d \) would be replaced by another “characteristic length” (e.g. by the diameter of the sphere with equivalent volume), and the numerical coefficient \( 3/2 \) subsequently would be modified.

If, at an appropriate wavelength, \( \lambda \), the algal cells are considered as practically non-absorbing particles, the attenuation (the sum of absorption and scattering) is due only to scattering. In terms of efficiency factors, \( Q_a, Q_b, Q_c \), respectively, for absorption, scattering and attenuation (with \( Q_c = Q_a + Q_b \)), such a situation corresponds to

\[
Q_a = 0 \ and \ Q_b = Q_c.
\]

For “soft” particles exhibiting an index of refraction, \( n \), close to that of the surrounding water, \( n_w \), the factor \( Q_c \) takes a simple form according to the anomalous diffraction approximation (Van de Hulst, 1957):

\[
Q_c (\rho) = 2 - (4/\rho) \sin \rho + (4/\rho^2)(1 - \cos \rho),
\]

where the dimensionless parameter \( \rho \), which combines the relative size, \( d/\lambda \), and the relative refractive index \( m = n/n_w \), is defined as

\[
\rho = 2\pi(d/\lambda_0) (n - n_w)
\]

or

\[
2\pi \ (d/\lambda) \ (m - 1),
\]

where \( \lambda_0 \) and \( \lambda \) are, respectively, the wavelength in vacuo and in water, and \( m \) is a real number (no absorption). The behaviour of the efficiency \( Q_c \) with increasing size (more
precisely with increasing \( \rho \) values) is well known (e.g. Van de Hulst, 1957). From zero, \( Q_c \) steeply increases until it reaches a first maximum at \( \rho = 4.09 \). Then \( Q_c \) undergoes a series of periodic oscillations with diminishing amplitudes centered on the asymptotic value of 2. If the particles are no longer equally sized but have a log-normal size distribution, the oscillations are smoothed or even annihilated (except the first one) and the asymptotic value is approached at lower \( \rho \) values (Brichaud et al., 1983).

As a first approach, it is interesting to examine this particular case when \( Q_c \) (=\( Q_b \)) is close to its limiting value of 2. Equation (1) reduces to

\[
b^* = 3/\sigma_c,
\]

and \( b^* \) appears related to the reciprocal of both size and internal chlorophyll concentration. Because of the size distribution (or the resulting smoothing effect), this approximate formula is valid for an extended range of size and not only for very large cells. It can be seen that \( Q_c = 2 \) when \( \rho > 7 \) (Fig. 7A, in Brichaud et al., 1983); with \( \lambda = 0.6 \ \mu m \) and \( m = 1.05 \), this \( \rho \) value corresponds to \( d \approx 10 \ \mu m \), meaning that the above relationship becomes applicable for cells with a diameter larger than this value.

The condition of non-absorption introduced above can be relaxed. The effect of absorption, everything else being constant, is to reduce the scattering capability. Therefore, inside an absorption band, when \( Q_a \) differs from 0, \( Q_b \) becomes less than \( Q_c \). Under the same proviso of high \( d \) (or \( \rho \)) values which lead to \( Q_c = 2 \), the limiting value for \( Q_a \) is 1; thus \( Q_b \) (=\( Q_c - Q_a \)) will also tend towards 1 (instead of 2 as before). Therefore \( b^* \) could be reduced, at most by a factor of 2, for sufficiently large and absorbing cells (see Fig. 2b in Morel and Brichaud, 1981b). These cells must be perfect “black bodies” to exhibit such an effect (leading to \( Q_a = 1 \)). In general, the lowering effect of absorption on \( b^* \), while being easily evidenced, remains much weaker (Brichaud et al., 1983). Even the most absorbing algal cells (e.g. Hymenomonas elongata, in the above reference) are not black bodies and \( Q_a \) remains less than 1.

When considering the whole size range, including small (<10 \( \mu m \)) phytoplankters, the variations of \( Q_b \) can no longer be ignored. The approximation (equation 3) has to be replaced by the exact expression:

\[
b^* = (3\pi/c_i\lambda)n_w(m - 1)Q_b(\rho)/\rho,
\]

which clarifies the links between \( b^* \) and the characteristics of the cell, i.e. its intracellular Chl \( a \) concentration, \( c_i \), its relative index, \( m \), and its size through \( Q_b(\rho)/\rho \) (or \( Q_c(\rho)/\rho \) if the absorption can be neglected). This equation deserves some comment, as the wavelength is considered as constant and chosen in such a way that absorption is negligible.

(i) \( b^* \) is obviously inversely proportional to \( c_i \) since when \( c_i \) increases, a smaller number of cells is required to get a unit concentration of pigment within the suspension.

(ii) For a given cellular material (implying \( c_i \) and \( m \) constant), \( b^* \) would reproduce the variations of the function \( Q_c(\rho)/\rho \) when the cell size is changing (see Fig. 1). The merit of this graph is that it shows the existence of two domains separated by the maximum occurring at \( \rho \approx 3 \) (2.934 for monosized particles and less for particles polydispersed in size). When \( \rho < 3 \), the behaviour depicted by equation (3) is reversed since a decrease in \( d \) presently results in a decrease in \( b^* \). Such a result is of interest when predicting the optical properties of picoplankton.

(iii) The relative index, through its increment with respect to water, \( m - 1 \), acts as a proportionality factor.
Fig. 1. Graph of the dimensionless quantity $Q_c(\rho) / \rho$ as a function of the dimensionless parameter $\rho$ (solid curve). The dashed curve is derived from the solid one by introducing a size distribution function [a log-normal distribution with a probability of occurrence of 1% for spheres having half or twice the diameter which corresponds to the maximum (100%) of probability]. By giving the relative index of refraction a value of 1.05, the scale (abscissa) is transformed into a diameter scale $\bar{d}$ (μm). By fixing the wavelength ($\lambda_0 = 0.6$ μm) and the intracellular chlorophyll concentration ($c_i = 10^5$ mg m$^{-3}$), a second ordinate scale can be constructed which gives the value of the specific scattering coefficient, $b^*$, in m$^{-1}$ (mg Chl a)$^{-1}$.

**METHODS**

The methods developed for growing the axenic strains in batch cultures, and for measuring their optical properties, their pigment concentration and size distribution were described in Bricaud et al. (1983) and Bricaud and Morel (1986). The results presented here have been extracted from these papers (species numbered 1–7 in Table 1). Systematic measurements of the same kind have been continued, and the results for the species 8–19 have been selected from data made available before publication, courtesy of A. Bricaud, A. L. Bedhomme and J. Gostan.

The cultures were incubated under continuous irradiance of 300–400 μE m$^{-2}$ s$^{-1}$ at 18°C. Irradiance of 400 and 25 μE m$^{-2}$ s$^{-1}$ were used for Isochrysis galbana (18a and 18b, respectively, in Table 1). The cyanobacteria strain (likely Synechocystis sp.) was isolated by J. Neveux (laboratoire Arago, Banyuls-sur-mer, France) and grown under 200 and 16 μE m$^{-2}$ s$^{-1}$ (19a and 19b, respectively).

Specific scattering values for freshwater phytoplanktonic algae also grown in culture have been recently published (Davies-Colley et al., 1986). From the Tables 2 and 3 in their paper it is easy to derive the intracellular concentration $c_i$ and the diameter of the equivalent sphere for three species (numbered 20–22 in Table 1).

**EXPERIMENTAL RESULTS**

The $b^*$ values for these 22 species are plotted as a function of their mean size, $\bar{d}$, in Fig. 2. The most common values for $b^*$ range between 0.1 and 0.2 m$^2$ mg$^{-1}$. The highest $b^*$ values are only associated with small sized cells (4–6 μm), but not all small cells exhibit
Table 1. Relevant information concerning the algae grown in culture which are used in Figs 2 and 4; $d$ is the mean equivalent diameter, $c$, the intracellular Chl a concentration and $b^*$ is the chlorophyll-specific scattering coefficient determined at the wavelength of minimum absorption. This minimum occurs in the 580-600 nm band for all species from 1 to 18. Due to the presence of phycocyanin, the minimum of absorption for the cyanobacteria (likely Synechocystis sp.) is shifted towards 540 nm. The $b^*$ values given by Davies-Colley et al. (1968) for species 20-22 are for $\lambda = 550$ nm.

<table>
<thead>
<tr>
<th></th>
<th>$d$ (10^{-9}m)</th>
<th>$c$ (kg m^{-3})</th>
<th>$b^*$ (m^{2} mg^{-1})</th>
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<tr>
<td>1</td>
<td>Tetraselmis maculata</td>
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</tr>
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<td>9</td>
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</table>

Fig. 2. Specific scattering coefficient $b^*$ at the wavelength of minimal absorption for several phytoplankters grown in culture, plotted vs their mean diameter $d$ (see Table 1). Triangles represent the values for 3 freshwater algae (Davies-Colley et al., 1986; species 20-22 in Table 1).
high values. Since no clear tendency emerges from this plot, size does not appear to be the dominant factor in determining $b^*$; the intracellular chlorophyll concentration $c_i$ is largely responsible for the dispersion of the points. This dispersion can be partially reduced by considering equation (4) from which it results that the product $c_i b^*$ must conform to variations of the number $Q_e(p)/p$, except for the residual effect of the potentially varying factor $(m - 1)$.

At a fixed wavelength ($0.6 \, \mu m$), and when $m$ is given various values, a family of curves can be generated which show the theoretical variations of $c_i b^*$ with $d$ (Fig. 3). For cells of large or moderate dimension ($>15 \, \mu m$) $m$ has a weak influence on $b^*c_i$. Conversely, for small algae ($<10 \, \mu m$) the refractive index appears to be of prime importance. For instance, for cells of a diameter about 4 $\mu m$, and with $c_i = 1.10^6 \, mg \, m^{-3}$, $b^*$ can vary from 0.2 to more than 1 $m^2 \, mg^{-1}$ when $m$ is increased from 1.02 to 1.06 (a reasonable range for biological material; AAS, 1981).

The experimental values $c_i b^*$ are plotted similarly against $d$ (Fig. 4). The dispersion of the points is considerably reduced when compared to Fig. 2. Moreover the position of the points inside the plane $d-c_i$, $b^*$ agrees remarkably well with the theoretical predictions displayed in Fig. 3. Because the index of refraction has not been independently determined, it is difficult to extend the comparison between these data and the individual curves in Fig. 3.

The experimental chlorophyll-specific scattering values have been found to vary over a somewhat unexpectedly wide range (0.06–0.6 $m^2 \, mg^{-1}$). The most striking observation at this point is probably that such a range is fully compatible with, and can be explained by, a simple theoretical treatment.

There is also a question as to whether the $b^*$ values obtained from algae grown in culture are similar to those for algae in the natural environment. In other words, it is

![Fig. 3. Theoretical variations computed from equations (2) and (4) for the product $c_i b^*$ (intracellular chlorophyll concentration and specific scattering coefficient) with the diameter $d$, for different values of the relative index of refraction $m$ and at a fixed wavelength ($0.6 \, \mu m$).](image-url)
necessary to examine to what extent the growing conditions could influence, or introduce a bias in, the chlorophyll-specific scattering by phytoplankton.

With few exceptions (18b–19b), algae were cultivated under fluorescent tubes providing an irradiance of ca. 350 &mu;E m\(^{-2}\) s\(^{-1}\) (or 155 &mu;E m\(^{-2}\) s\(^{-1}\) in the Davies-Colley experiment). This level corresponds to roughly 25% (or 10% resp.) of the solar irradiance at the sea surface for high solar altitude. At lower irradiance level phytoplankton generally respond by increasing the chlorophyll content per cell (e.g. Falkowski, 1980; note that this trend is also detectable by the change in \(c_i\) for the paired experiments 18a and b or 19a and b). Any increase in \(c_i\) results in lowering \(b^*\). Considering the moderate radiative levels used for the cultures, such an effect is not expected and the \(b^*\) values presented above are therefore believed to be comparable with the *in vivo* values in the euphotic layer, at least in its upper part. It has to be pointed out that \(c_i\), which is the parameter responsible for most of the variability in \(b^*\) (Fig. 2), is perhaps more variable in natural assemblages. With a wider range of variations in nutrient and light availability, or in physiological state, \(c_i\) and therefore \(b^*\) may experience larger changes in the natural environment than those reported for healthy cells grown in steady and favourable conditions. This remark does not prevent us from comparing *in vitro* and *in situ* values.

**Comparison with Chlorophyll-Specific Scattering in the Natural Environment**

During several cruises (see references in Gordon and Morel, 1983), the scattering coefficient of the seawater, \(b\), was determined *in situ* at 550 nm and the Chl a concentration, \(C\), was measured on samples collected at the same depth. These data allow the relationship between both these parameters to be studied. Such a study is meaningful only if “Case 1” waters are considered; that is oceanic waters for which
phytoplankton and their derivative detrital products play a dominant role in governing the optical properties (sediment concentrations are low). As shown in Fig. 5a, b and C appear to be linked by a non-linear relationship over three orders of magnitude in chlorophyll concentration. GORDON and MOREL (1983) have proposed an expression for this relationship

$$b = 0.30 C^{0.62}.$$  

Fig. 5. (a) Scattering coefficient $b$ (m\(^{-1}\), at $\lambda = 550$ nm) measured in situ within the euphotic layer vs pigment concentration $C$ (Chl $a$ + phaeophytin $a$ in mg m\(^{-3}\)) measured on samples from the same depth. Turbid waters are excluded, only the points (506) corresponding to Case 1 waters are shown (redrawn from GORDON and MOREL, 1983). Both scales are logarithmic. (b) “Natural” chlorophyll-specific scattering coefficient in marine environment, $b/C$, deduced from the data presented in (a), and plotted vs the pigment concentration $C$ (log-scale).
The band delimiting Case 1 waters is between the lower limit
\[ b = 0.15 C^{0.62}, \]
and the upper limit
\[ b = 0.45 C^{0.62}. \]
which is somewhat arbitrary. Such a non-linearity in the \( b-C \) statistical relationship implies that the "natural" specific scattering coefficient, also defined as \( b/C \), would change regularly with the actual chlorophyll concentration in the sea according to
\[ b/C = 0.30 C^{-0.38}. \]

The enhancement of \( b/C \) for decreasing \( C \) values is shown in Fig. 5b.

It must be pointed out that for mesotrophic or eutrophic waters (\( C \) from 0.5 to more than 10 mg m\(^{-3}\)), the \( b/C \) values in natural environment (from 0.5 to 0.05 m\(^2\) mg\(^{-1}\)) are within the range of the \( b^* \) values measured in vitro. The lowest natural \( b/C \) values (\( \approx 0.1 \) m\(^2\) mg\(^{-1}\)) typical of eutrophic waters necessarily imply the dominance of large cells with rather high intracellular pigment concentration (see equation 3). In addition, such low \( b/C \) values suggest that the light scattering process in these kinds of waters must be almost exclusively ensured by the algal cells themselves. Consequently the other (detrital) particulates have a restricted contribution to the scattering properties of these waters.

In oligotrophic zones (with \( C < 0.1 \) mg m\(^{-3}\)) the \( b/C \) values become very high (\( > 0.8 \) m\(^2\) mg\(^{-1}\)). According to the theory, it could be tempting to interpret these values as the result of the predominance of small sized phytoplankters with relatively low \( c_i \) values. If the first point should agree with the recent evidence that picoplankton form an important fraction of the algal biomass in oligotrophic ocean (e.g. PLATT et al., 1983), the second point (the low chlorophyll inner concentration) is far from being proved. In any case such an interpretation is hazardous at least for two reasons:

(i) The GF/C Whatman filters used in the experiments reported in Fig. 5 are not fully efficient in retaining tiny cells. If picoplankton were present, the Chl \( a \) concentration might have been underestimated and therefore the chlorophyll-specific coefficient overestimated.

(ii) In Case 1 waters, the scattering coefficient, \( b \), results from the presence of not only living algae, but also, associated debris. When dividing \( b \) by \( C \), the "natural" \( b^* \) value obtained is therefore an overestimate of the "true" chlorophyll-specific scattering coefficient for algae only. Since the relative proportions of detritus to living cells may vary, so will the overestimation. As seen previously, this effect apparently is negligible for eutrophic waters with relatively low detritus. Some arguments, however, suggest that the ratio of detrital to living materials would increase when the pigment (or algal biomass) concentration diminishes (see GORDON and MOREL, 1983). Therefore the \( b/C \) values would be enhanced in oligotrophic waters, although this enhancement does not mean that the true specific coefficient of the living algae is considerably increased.

**DISCUSSION AND CONCLUSIONS**

The \( Q_c \) expression used in equation (2) is valid for spheres. For other shaped and randomly oriented particles \( Q_c \), as a function of a size parameter analogous to \( \rho \), is
somewhat but not fundamentally modified (Aas, 1984). Hence the \( Q_c(\rho)/\rho \) curve keeps
the same general pattern. Moreover this pattern is simplified by the smoothing effect
which occurs when the particles include a wide range of sizes (see dashed curve in Fig. 1).
Therefore polydispersed systems of spherical or non-spherical particles cannot behave
very differently, and the dependency of the quantity \( b^*c_i \) upon an equivalent diameter
(as in Fig. 3) remains essentially unaffected. In equations (1) and (4), in addition to \( Q_c \),
another parameter comes into play, the ratio \( s/v \) of the cross-sectional area to the
volume. Irregularly shaped particles always exhibit \( s/v \) ratios higher than those of spheres
of equal volumes. Therefore equations (1) and (4), which provide a lower limit for \( b^* \),
can serve as a good approximation for diversely shaped cells, assuming they are
sufficiently compact bodies. Departures (i.e. underevaluation of \( b^* \)) can however be
expected for elongated or extended discoidal organisms.

Another assumption which has been made considers the algal cells as homogeneous
bodies. From this assumption it results that a single (mean) index of refraction can be
assigned to the cells. When considering that the various constituents of algae have similar
refractive indices (relative to water), this hypothesis is a reasonable first approximation.
According to the thorough review in Aas (1981), \( m \) is of the order of 1.10 for lipids,
1.15 for carbohydrates, 1.20 for proteins, 1.15 for opal (diatoms) and 1.19 for calcite
(coccolithophorids). The mean or “bulk” index of algal cells, however, is much lower.
Mainly in response to the high water content rather than to the chemical composition the
expected range of variations for \( m \) could be 1.015–1.075. The inner refractive heteroge-
neities probably cause small departures with respect to the scattering properties pre-
dicted for homogeneous particles. These possible effects are out of the scope of the
present study, and this paper only attempts to show that a simple theory can account for
the general features which were evidenced by in vitro experiments.

If the concept of a bulk index is accepted, it is conceivable that a comparison of the
experimental data in Fig. 4 with the theoretical curves in Fig. 3 could provide an estimate
of this parameter, at least in the case of small algae sensitive to its value. Ambiguities are
unavoidable as the curves in Fig. 3 are intermingled and not monotonous; therefore \( m \)
values obtained by this simple way cannot be ascertained. Such a comparison is
nevertheless the rationale for determining a plausible value for the bulk index. If the
investigation is not, as here, restricted to the wavelength of minimal absorption (i.e. if \( Q_b \)
can be predicted for all wavelengths, even for those where absorption occurs), the same
reasoning can be repeated for each \( \lambda \). The constraints become stronger when the whole
spectrum is considered and the ambiguities in most cases are eliminated. Thus, a value of
the mean index of refraction for the whole cell, seen as an homogeneous body, can be
deduced (Briculaud and Morel, 1986).

As an example taken from this reference, the relative index obtained for Emiliania
huxleyi is 1.044. The calcified plates (coccoliths) typical of this species do not enhance
significantly its mean index. Its rather high chlorophyll-specific scattering (see Table 1)
originates mainly from its low \( c_i \) value and partially from its size, close to that for which
the maximum of the \( b^* \) curve occurs (see Fig. 1). With a backscattering ratio, \( b_b \), less
than \( 3.5 \times 10^{-3} \), these algal cells however cannot produce a significantly high backscatter-
ing (per unit of chlorophyll). The high reflectances observed in the satellite imagery
(Holligan et al., 1983) for coccolithophore-dominated waters likely originate from the
numerous detached coccoliths rather than from the living cells themselves.

In conclusion, when considering the intricate influences of \( c_i \), \( d \), and \( (m - 1) \) upon \( b^* \),
this coefficient is expected to vary in a wide range. The observed range for species grown
in culture is 0.06–0.6 m² mg⁻¹. It is fully compatible with the experimental values of \(c_i\) and plausible values for \((m - 1)\), when these values are combined in a simple theoretical
frame. The simplifying assumptions adopted in this theoretical approach do not preclude a
global understanding of the bulk scattering properties of algae. By keeping in mind that
in any case \(b^*\) is inversely proportional to \(c_i\), the effect of the size on the quantity \(b^* c_i\)
(Figs 1 and 3) can be summarized as follows: (i) picoplankters (with \(d < 2 \mu\)m) exhibit
low \(b^* c_i\) values, which decrease as the size decreases. \(b^* c_i\) depends on, and, increases
with \((m - 1)\). (ii) Small phytoplankters (in the range 3–8 \(\mu\)m) are the algae for which the
highest \(b^* c_i\) values can be expected. These values, strongly dependent on \((m - 1)\),
increase with increasing refractivity. (iii) Larger phytoplankters (>10 \(\mu\)m) exhibit low \(b^* \)
c\(c_i\) values, whatever their index. The approximation of equation (3) applies and \(b^* c_i\) is
inversely related to the size.

This approach also provides a clue in interpreting the links between the scattering
coefficient of a water mass and its algal content. A comparison with the field data shows
that the scattering coefficient of waters in eutrophic zones is mostly determined by the
phytoplanktonic cells themselves (and not by detrital material). In addition, the respon-
sible algae must have low \(b^*\) values (large cells with high pigment content). Conversely,
in oligotrophic areas, the scattering coefficient of water likely reflects the presence of
(relatively) abundant detritus, except if the systematic presence of highly refractive,
small-sized and low-pigmented cells could be ascertained. Finally, if in addition to the
routine measurement of chlorophyll, cell enumeration (and identification) and size
determination could be effected more frequently, when combined with a better know-
ledge of \((m - 1)\), these data would be useful. They are the parameters needed to use the
predictions from equation (4). Therefore it should be possible to infer the exact part of
the scattering coefficient of a water body which is due to the presence of algae. By
comparing the result to the fields values, an estimate of the ratio of living algae to their
detrital retinue could be deduced.

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Note added in proof

In the Introduction it was pointed out that the chlorophyll-specific scattering coefficient has been scarcely studied. This situation is rapidly changing. Very recently A. D. Weidemann and T. T. Bannister (1986, Absorption and scattering coefficients in Iredonquoit Bay. Limnology and Oceanography, 31, 567–583) have published data obtained in an eutrophic lake. Their values for this coefficient, in the range of 0.05–0.15 m² (mg Chl a)⁻¹, corroborate those derived from the present Fig. 5b for eutrophic waters.